SPECIAL CIRCULAR 100 JUNE 1974

Survival of Plant Pathogenic Bacteria

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CONTENTS

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ACKNOWLEDGMENTS

Thanks are extended to G. C. Daft, H. A. J. Hoitink, P. O. Larsen, T. D. Miller, J. P. Sleesman, and L. E. Williams for constructive criticism of the manuscript.

AGDEX 630 6-74-2M

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CURT LEBEN[2]

INTRODUCTION

Plant diseases incited by bacteria are not as numerous as those incited by fungi and viruses, but many (probably most) plant species can be attacked by bacteria at one or more stages in the plant life cycle. Some bacterial diseases are of great economic importance; e.g., the vascular wilts of musaceous, solanaceous, and other hosts (incited by *Pseudomonas solanacearum*), fireblight of rosaceous plants (*Erwinia amylovora*), and the bacterial blights of cotton and rice (*Xanthomonas malvacearum* and *X. oryzae*). Crops of lesser importance also may be limited because of the depredations of bacterial pathogens.

It is useful to consider how plant pathogenic bacteria survive during unfavorable periods, particularly season-to-season periods. This publication adds to the excellent efforts of the most recent reviewers of this subject, Buddenhagen (7), Crosse (11), and Goto (25). Buddenhagen and Crosse stressed survival in the soil and Goto emphasized survival in relation to vegetation. In this publication, an attempt to link survival at both sites is presented. An abstract of this paper has appeared (39).

When bacteria are considered as a whole, the subject of bacterial survival is very large indeed, but when plant pathogenic bacteria are considered, surprisingly little work has been done on this part of the life cycle. Three constructs—frameworks of fact and speculation—concerning survival are offered in this paper. These are based on work with plant pathogenic and other bacteria. It is hoped they will offer a degree of integration and will be useful in suggesting further research.

Bacterial pathogens must survive, of course, or the diseases they incite would have vanished long ago. It is natural that much effort has been devoted to the pathogen growth stage—the multiplication phase—of the life cycle. After all, the products of bacterial growth are seen: the wilts, the blights, the leaf spots, and all of the imperfections resulting in greater or lesser losses. More and more, plant pathologists are trying to refine understanding of life cycles and modes of survival. This knowledge may well lead to improved disease control.

There is no need to belabor a useful principle of plant and animal pathology: if possible, one should attack the pathogen during diminished

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[1]Based on a lecture presented before the Second International Congress of Plant Pathology, University of Minnesota, Minneapolis, Minn., U.S.A., Sept. 6, 1973. Literature survey was completed June 1, 1973. Accepted for publication January 4, 1974.

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survival times. With the plant pathogen, the low population point usually is between seasons. In this paper, season-to-season survival is referred to as "long-term". "Short-term" survival means survival for minutes to days.

References to spore-forming bacteria, which do not appear to be important plant pathogens, are excluded. Survival in arthropods is also excluded. There are comparatively few instances of long-term survival of conventional bacteria in these animals. However, recent studies on "spiroplasmas" (16) and "rickettsia-like" bacteria (24) suggest that survival of unusual forms in arthropods is greater than previously suspected. Then, too, "mycoplasma-like" organisms, which most resemble bacteria, survive in insects.

At least two other important topics related to survival are mentioned only in passing. These are: methods used to detect survivors, and the exchange of genetic entities between pathogenic and nonpathogenic bacteria associated with plants. Recent papers covering assay methods have been written by Beech and Davenport (3), Dickinson (18), and Goto (25). Gibbins (23) has discussed genetic relatedness with respect to the origin of plant pathogens. In this connection, Starr and Chatterjee (73) have hypothesized that saprophytic *Erwinia* spp. or Erwinias associated with plants may be the source of the Erwinias producing diseased conditions in man and other animals.

SHORT-TERM SURVIVAL

Plant pathologists are mostly concerned with the practical effects of long-term survival. However, it is appropriate that attention be given here to the survival of metabolically and physically active bacteria for shorter periods—hours to days. Physical, chemical, and microbiological factors affecting short-term survival also affect long-term survival, but information about long-term survival is much more sketchy.

A brief discussion of inanimate and animate factors affecting short-term survival of bacteria is appropriate.

Inanimate Factors Affecting Survival

Water governs the life of bacteria in vital ways and has a marked effect on short-term survival. Free water probably is necessary for the multiplication of bacteria in general, and it is of course required for swimming. Metabolically active forms of most bacteria are killed by drying, but there are differences in degree owing to species and conditions of drying.

Active plant pathogenic bacteria existing independently probably die quickly when they are dried, as would be expected of nonsporing bacteria in general. There appears to have been no systematic study of plant pathogenic bacteria in this respect, however. Some 70 years ago, Jones (30) and Smith (71) placed active cells of pathogens in drops on cover slips. Slips were dried and assayed later *in vitro.* Results indicated that season-to-season survival was unlikely and that survival depended on conditions of drying. Jones found that a potato soft rot bacterium he studied died within minutes when water suspensions were dried. Work by Kauffman and Leben with *Pseudomonas glycinea* suspended in buffer demonstrated that ca.10^6 cells per ml. of this pathogen died virtually as soon as drops of suspension dried on cover slips (unpublished). Another recent example of sensitivity to desiccation is that of Kikumoto and Sakamoto (36), who found that *Erwinia aroideae* cells died rapidly when soil particles colonized by this pathogen were dried.

The relative humidity during drying influences survival of many kinds of bacteria. For example, *Erwinia amylovora,* in common with the intensively studied *Escherichia coli,* survived best at 40-90% relative humidity in air-borne particles (72). A number of works indicated that a low relative humidity limits multiplication of many kinds of macro- and microflora on the plant surface, including plant pathogenic bacteria. On the other hand, high humidity favors epiphytic growth in general (43).

Swimming may be far more important for survival of plant pathogenic bacteria than present information suggests. Movement toward or away from a stimulus is an important fitness factor for many organisms which swim. Many pathogenic bacteria are motile, and some experiments have indicated they move toward seemingly favored positions (58, 62, 69, 80). It is not difficult to envision a bacterium and its progeny swimming in a drop of water on a leaf toward a source of nutrients (attractants) and that this location may provide a survival site, as suggested below.

Repellants as well as attractants may help "guide" swimming bacteria (74, 76). The swimming of avirulent *Pseudomonas solanacerarum* isolates appeared to be a fitness factor not for *in vivo* growth but for *in vitro* growth, because Kelman and Hruschka (35) found that virulent isolates were not motile. The subject of swimming of plant pathogens needs much more investigation.

Numbers of plant pathogenic bacteria exposed on the above-ground parts of plants probably are quickly reduced by the ultraviolet (UV) rays in sunlight. Inactivation by UV is influenced by relative humidity (65) and other factors. Death from UV must be very large when pathogens washed from aerial lesions are spread widely during a wind and rain storm. Many years ago, Jones (30) discovered the sensitivity of the soft rot bacterium he studied to sunlight and recommended exposing potato tubers to sunlight as well as to drying conditions for disease control.

There is much literature on the effects of UV and relative humidity on the survival of bacteria. Little work has been done with plant pathogens, however.

In addition to water and sunlight, two other inanimate factors, temperature and the chemical environment at the survival site, undoubtedly have a profound influence on pathogen survival. They also influence other microorganisms, especially if water is present and the chemicals serve as nutrients for these organisms.

The interactions among inanimate factors are varied, complex, and little studied with respect to their influence on the survival of pathogens.

Animate Factors Affecting Survival

Prior to and during infection, and with the aging of a lesion, pathogenic bacteria are subject to manifold pressures exerted by other microorganisms. Probably the only time when a pathogen is free, or nearly free, from influences of these other organisms is during the early invasive growth period within plant tissue. As a lesion ages, especially in a moist environment and especially in contact with soil, omnipresent nonpathogenic microorganisms begin the decomposition of the lesion and the masses of pathogen cells it contains. In addition to the microflora, many kinds of fauna may be present, and some of these consume bacterial pathogens. It is probable that in regions where plant tissues decompose rapidly, the survival time for a pathogen is shorter than in regions where decomposition of organic materials takes place more slowly.

Evidence reviewed above suggests that the life expectancy of metabolically active, independent cells of pathogenic bacteria likely is a short one. Consider the soil environment. Assume that a bacterium began its independent existence by being washed from a leaf lesion into the soil or by swimming from a colony near a root. Gray and Williams (26) reviewed work suggesting that microorganisms in the soil are largely inactive, owing to the sparsity of energy sources and to other unfavorable factors. More recently, Brown (6) presented additional evidence that bacterial members of the soil flora are in a state of reduced metabolism most of the time and refers to this condition as "bacteriostasis", a term parallel to "fungistasis" (78).

An immigrating pathogen would encounter these adversities. If an energy source should become available, very likely other organisms would be better able to use it, because many plant pathogens are not nutritionally versatile (57, 66). Other organisms would possess a greater "relative competitive advantage" with respect to energy sources, to use the term of Cook and Papendick (9). Thus, it seems likely that unless a suitable niche could be found quickly, immigrating cells of bacterial pathogens in the soil environment would expire within a short time.

Yet some pathogens are "soil borne" and do persist in soil for years. These are mentioned below.

Life expectancy of active, independent cells of a pathogen in an aerial environment also would be expected to be short. In Ohio climate, bacteria washed from an active lesion on a leaf to another area of the foliage probably would die soon, owing to desiccation or UV irradiation. If the cell did not meet this end, it then would face the competition of other organisms already living on the plant. Crosse (12), Gibbins (23), Last and Warren (37), and Leben (43) have written about the relationships among epiphytic organisms. A notable symposium covering many aspects of the microbial ecology of the leaf surface was held in 1970 in Newcastle (63).

CONSTRUCTS

Three constructs are offered as a framework for thinking about the survival of plant pathogenic bacteria.

1. Long-term survival of pathogens in nature takes place only in association with living or dead plant tissues. This is a "critical trait" (1) which allows pathogens to survive in the face of recurrent or occasional stresses.

2. Long-term survival is not likely to take place unless cells of the pathogen are in aggregates or unless they are associated with living plant tissues in "protected positions".

3. Pathogens in a state of reduced metabolism are more likely to survive than are active cells.

HYPOBIOSIS

Bacterial cells in a state of reduced metabolism are designated hypobiotic cells. The term is taken from the microbiological literature (52) and has had little use in plant pathology. Yet the concept bears special significance. In the hypobiotic state, microorganisms may live long periods without added nutrients and are more likely to survive the physical and chemical stresses causing death than when metabolic activity is high. Hypobiosis can be induced experimentally by low temperature, loss of water, increasing salt concentration, and a variety of other means.

It seems reasonable to conclude that pathogens surviving for long periods are in a hypobiotic condition, having arrived at that state as a result of the natural processes taking place with the aging of diseased tissues. Hypobiotic cells would be the survivors in dry leaf, stem, and root lesions of annual plants: they would represent a small portion of the masses of cells once alive within the lesion. Hypobiotic cells are, of course, quite different from actively metabolizing ones, and they de-serve much more study than has been given them. For example, cells of *Pseudomonas aeruginosa* were more sensitive to desiccation in the exponental growth phase than when cells were 7 days old (70). Normand *et al.* (60) found that the morphology of *Pseudomonas phaseolicola* cells was different in the lesion center than at the lesion edges, where the bacteria were younger.

LONG-TERM SURVIVAL

Some bacterial pathogens can survive for many years if they are in diseased plant tissues which are dry, as is well known. The surviving cells in these tissues, in addition to being in a hypobiotic state, probably are protected in varying degrees by the surrounding masses of dead bacterial and plant cells and by products of the pathogen-host interaction.

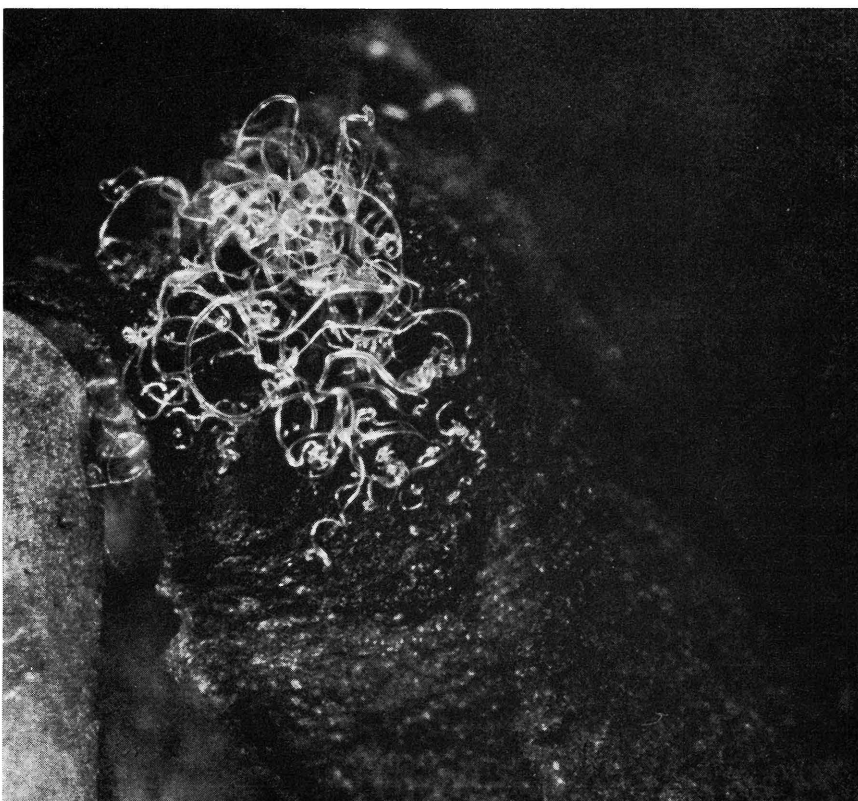

FIG. 1.—The filamentous form of exudate oozing from a cotyledon lesion incited by Pseudomonas glycinea. **Exudates consist of masses of bacteria in a matrix.**

On the other hand, some pathogens die when the lesion dries (31, 61). If a pathogen survives in the dry lesion and the lesion is moistened and exposed to microbial decomposition, as in soil, it is anticipated that surviving cells surrounded by a quantity of diseased tissue would not be as readily decomposed as when imbedded in smaller amounts. Furthermore, cells within tissues would be less subject to decomposition than those in soft tissues.

Debris from diseased plants must always be considered a possible source for seasonal carryover. However, two questions should be asked. How likely is it that debris will decompose between seasons? If it is not decomposed, what is the likelihood that surviving pathogen cells will come in contact with susceptible plant tissue? In working with *Pseudomonas glycinea,* for example, it was found that overwintering in quantities of diseased leaves was poor in soil, better on sod, and better yet if diseased leaves were suspended in air (14). The differences are attributed to the amounts of moisture and the relative numbers of decomposing microorganisms at the three sites. With ordinary crop cultivation methods, survivors in diseased leaves probably would occur near susceptible seedlings rarely (if ever), particularly if crops were rotated.

On the other hand, diseased debris associated with seed likely would be kept dry and thus not subject to deterioration. In this condition, cells of a pathogen may well survive as long as the seed is viable. Baker (2) has reviewed all aspects of seed pathology. This is an important subject, because survival with seed is responsible for much damage produced by bacterial pathogens of annual crops.

Lesion exudate is another type of debris resulting from disease. Exudates consist of masses of pathogen cells in a matrix, which may harden. Thus with *Erwinia amylovora,* exudate in the form of strands may disseminate the pathogen via air currents within the orchard (33). Survival in dry strands for months has been reported.

Exudates are produced in lesions incited by many pathogens. For example, when bead-shaped exudates of *Pseudomonas glycinea* were moistened, they were dispersed and formed flakes when dried (15). Flakes could be disseminated locally by the wind. It is suspected that long-term survival of pathogens in exudates in nature is not common, though, because most exudates would be degraded by physical or chemical action, or they would become moistened and destroyed by microorganisms.

PROTECTED POSITIONS

It is clear that many bacterial pathogens survive well under some conditions if they are in aggregates. As indicated, they probably die quickly as individuals in soil or on exposed sites above ground. However, recent evidence suggests that individuals or a few cells can survive for varying periods of time in association with the healthy living plant or plant part, at sites termed "protected". It is emphasized that plant tissues are healthy as far as can be determined.

The protected position hypothesis first was deduced by experiments in which water drops were placed on healthy cucumber leaves, and the areas covered by these drops were examined later for bacteria (46, 47). Sizeable populations of nonpathogenic bacteria developed in 48 hours in many drop areas. In contrast, few bacteria were present in areas not covered by drops. It was concluded that the progenitors of these bacteria were in some sort of sheltered locations on the leaf surface before drops were placed over them. Probably they were hypobiotic. Blakeman (4) and Blakeman and Fraser (5) also obtained a rapid buildup of epiphytic bacteria in water drops on leaves of two plant species.

The bacteria just discussed were nonpathogenic. Recent work suggests that pathogenic bacteria also survive in protected positions on healthy leaves. Mew and Kennedy (55) found that *Pseudomonas glycinea* multiplied and survived for at least 14 days on healthy soybean leaves in the greenhouse. Scherff (67) and Kauffman and Leben (unpublished) confirmed these results. In the latter tests, three levels of relative humidity were used; multiplication and survival were observed at each level: low, medium, and high. Multiplication or survival at the low relative humidity was not expected because *P. glycinea* is sensitive to drying and epiphytic growth of all types is reduced by a low relative humidity (43). Consequently, it was concluded that the pathogen multiplied in a protected, moist site and survived at or near this location. Other workers have found pathogens surviving on healthy host or nonhost leaves (10, 13, 22, 28, 32, 64, 77).

From these examples, one may extend the hypothesis of protected positions to other locations associated with the healthy living plant or plant part. For example, a few hypobiotic cells of a pathogen within a seed would be in a well-protected and significant survival site. Buds may be protected survival sites (41), and pathogens may survive within fruit tree stems (8, 34). The short report of Meneley and Stanghellini (54) indicated that the interior parts of a number of fresh vegetable products served as protected survival sites for bacteria which caused tissue decomposition when these products were warmed.

The rhizosphere also may serve as a protected position for the survival of some pathogenic bacteria. Pathogens have been found associated with apparently healthy roots of host and nonhost plants. Goto (25) has reviewed this literature, much of which is in Japanese. Possibly these pathogens are living in the mucigel surrounding the root (27).

It seems significant that most pathogens do not survive well in soil, and the few that do persist, the soil-borne pathogens, possess wide host ranges.

Assume that a soil-borne pathogen is able to occupy a niche on the rhizoplane of healthy host or nonhost plants. Pathogens at this location then could exist in soil for as long as there were roots of suitable species to provide sites for multiplication and survival. If suitable crop or weed plants were not grown, the pathogen would disappear. Unless plants became diseased, with the subsequent release of large amounts of inoculum, populations probably would remain at relatively low levels. A pathogen of this sort could be distributed in soil by contact between roots, by moving water and agricultural implements, by swimming, or by nematodes (29) and other fauna.

A parallel with *Rhizobia* spp. is evident here. Rhizobia grow and survive in association with nonhost as well as host roots, and it is suggested that they survive in the soil as long as these roots are present (19). If this suggestion is correct, an explanation is offered for the long-term disease potential of certain pathogens in the soil in the face of what is described as a hostile environment.

Protected positions probably are most significant for low numbers of cells of either pathogenic or nonpathogenic bacteria. However, it is possible that large numbers also could survive at these locations.

CONTRIBUTIONS OF THE PATHOGEN LIFE CYCLE PHASES TO SURVIVAL

The life cycle of a plant pathogenic bacterium may be divided into four phases or stages. These are the pathogenic, resident, saprophytic, and survival phases. The first three—pathogenic, resident, and saprophytic—are growth phases. What is the contribution of each in producing surviving cells?

Pathogenic Phase

As far as known, the pathogenic phase, in which there is a large increase in numbers of pathogen cells and the production of symptoms, contributes most of the cells entering a seasonal survival period. The larger the population of a pathogen entering the period, the greater the chances for survival, other conditions being equal. Large populations would be produced by compatible isolate-host combinations (those resulting in typical disease responses); incompatible combinations (resistance responses), which produce lower populations, would be much less likely to yield surviving cells.

Resident Phase

A decade ago it was suggested, on the basis of work with *Xanthomonas vesicatoria,* that some pathogenic bacteria possessed a "resident phase" in their life cycle. This was defined as the capacity for multiplication on the surface parts of the healthy shoot system (44). A revised definition is offered below.

It now appears as a result of recent studies that a number of bacterial pathogens possess a resident phase, which may be associated with leaves, buds, or flowers of host or nonhost plants (17, 20, 21, 22, 28, 38, 49, 50, 51, 53, 55, 56, 59, 67, 75). Earlier work is cited by Leben (43). *Pseudomonas syringae,* which has a wide host range, is the subject of most of these papers. Many leaf-spotting pathogens may be residents under

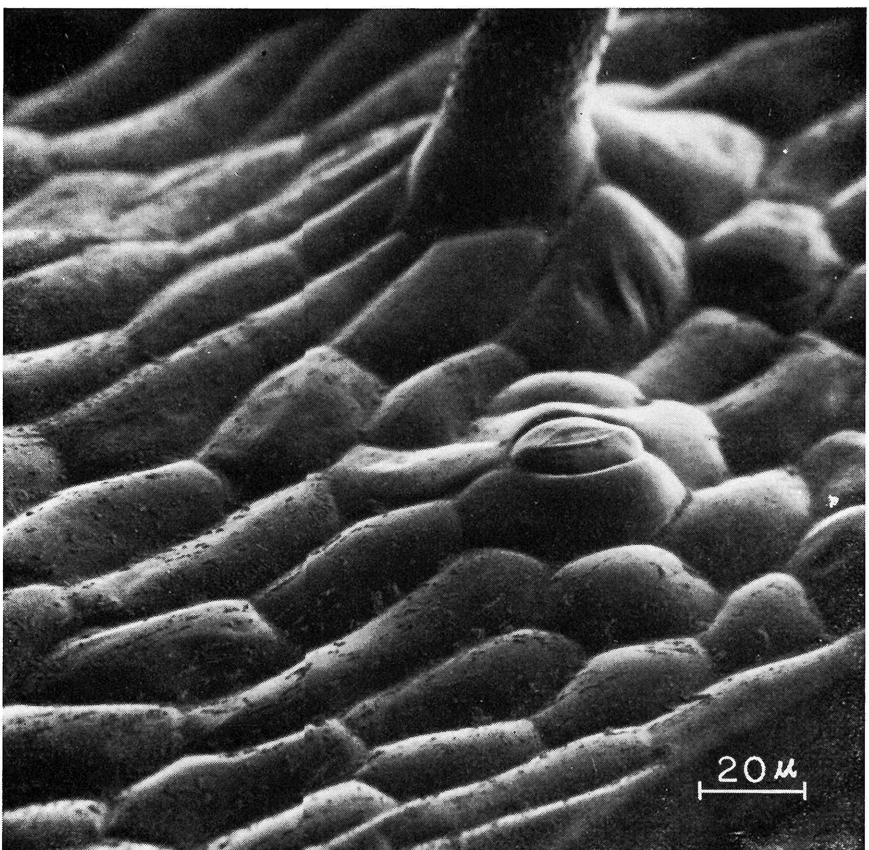

FIG. 2.—A scanning electron microscope view of the surface of a soybean stipule, showing pillow-shaped epidermal cells, the base of a trichome, and a stoma. Most of the small projections on the epidermal cells are aggregates of bacteria. These organisms also are found in abundance in depressions between epidermal cells, especially near the base of trichomes. These locations are possible protected survival positions.

some conditions. The increase of a pathogen in the absence of symptoms may be of epidemiological importance by serving to build up an inoculum as an immediate prelude to infection. That increase also could provide pathogen cells which survived unfavorable times. Probably survival sites would be at or near multiplication sites.

The location of these sites is speculative, but there are several possibilities. Leaves have been studied the most. In Ohio, relatively few nonpathogenic bacteria were detected on leaves of field plants (47). This suggests that these organisms, and likely pathogenic bacteria as well, survive in protected positions. Probably there is a periodic (possibly diurnal) rise and fall in numbers of emigrants swimming or being washed from these sites, with population levels being governed primarily by the amount of water on the leaf, duration of periods of wetness, relative humidity, and exposure to sunlight. The leaf surface, especially within deep, moist depressions between epidermal cells, probably is a multiplication and survival site. The underside of the leaf would be expected to have more protected positions than the exposed upper surface. The substomatal chamber and associated tissues also are suspect locations (79). However, water does not readily enter stomatal pores (68). Protected positions may be associated with trichomes (42) or with hydathodes or other natural openings. These hypothetical locations could be occupied by pathogenic and nonpathogenic bacteria. In addition, pathogens may multiply and survive unnoticed as a result of an arrested infection of a few epidermal cells. More work is needed to understand what is taking place, particularly with pathogens.

Buds also are worthy of comment as sites of multiplication and survival of pathogenic bacteria (41). In contrast to leaves in Ohio, the bud habitat (the gemmisphere) of some plants may carry a high population of a varied bacterial flora. The numbers and variety of nonpathogens in soybean buds, flowers, and young fruits were remarkable (40). Recently a *Pseudomonas syringae* type was found among the many bacteria in buds of healthy field soybean plants. Curiously, this pathogen produced progressive lesions on the soybean hypocotyl and cotyledon, but only incited a resistance response on leaves (49).

Saprophytic Phase

Do plant pathogenic bacteria have a true saprophytic stage in nature? Are pathogens able to grow—multiply—on dead tissue derived from either host or nonhost plants? Can pathogens multiply on other material in natural habitats? Some pathogens in aggregations readily survive in dead host tissue, as has been seen, but do they increase in these tissues? No direct evidence is known for the proposition that they do increase. On the other hand, there is much evidence that populations decrease. With the soybean blight pathogen, for example, once leaf lesions became necrotic, the pathogen population decreased. This took place if leaves were left on the plant or if they were detached and placed in soil or other natural situations (14, 50).

Probably saprophytic growth has been suspected to take place most often in soil. If the explanation proposed above for long-term persistence of soil-borne pathogens is accepted, saprophytism would not be essential for survival. In general, soil seems to be particularly inhospitable for bacterial pathogens, as has been mentioned. Consequently, it appears that true saprophytic growth in this medium is limited. If so, it would have little effect on survival. Obviously, more needs to be known about this difficult subject.

TERMINOLOGY

In 1961 "resident" was defined as a member of the microflora multiplying on the surface of the aerial parts of the healthy plant proper (45). Bacterial residents may be detected readily on the plant surface with suitable techniques. However, the possibility that some bacteria are within the plant and reach the surface through openings is difficult to exclude. In any event, workers have used "root resident" or "internal resident". Consequently, it is now proposed that the term resident be expanded to include all types of associations of microflora with healthy plants. This includes the surface and interior parts, above and below ground. Perhaps this alteration will avoid confusion. No strong brief for the original term or this expansion is held; some may find it useful, however, to have a short designation for an important ecologic grouping of the microflora. With this terminology, a pathogenic bacterium could possess pathogenic, resident, and saprophytic phases in its life cycle, as has been indicated, but the resident phase would not be restricted to the shoot surface.

CONCLUSIONS

Plant pathogenic bacteria are poorly adapted for survival in nature away from plant tissues. They are likely to survive seasonal periods in aggregates in association with dry diseased plant tissues, or as individuals or a few cells in protected positions associated with the healthy living plant or plant part. Surviving cells likely are in a hypobiotic state rather than in the active, vigorous conditions most often studied in the laboratory.

In nature, the pathogenic phase of the life cycle probably contributes most of the cells carrying the pathogen through adverse periods. The contribution of the resident phase may well be important, but the extent of its natural occurrence is unknown. On the other hand, the saprophytic phase seems to contribute few cells which survive.

If these ideas have validity, it is clear that further studies are needed, especially of hypobiosis, and the nature of protected survival sites and how pathogens get into them. With more understanding, plant pathologists may learn how to alter hypobiosis and to expose protected positions to advantage.

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Ohio's 110,000 farm families benefit from the results of agricultural research translated into increased earnings and improved living conditions. So do the families of the thousands of workers employed in the firms making up the state's $8 billion agribusiness complex.

But the greatest benefits of agricultural research flow to the millions of Ohio consumers. They enjoy the end products of agricultural science —the world's most wholesome and nutritious food, attractive lawns, beautiful ornamental plants, and hundreds of consumer products containing ingredients originating on the farm, in the greenhouse and nursery, or in the forest.

The Ohio Agricultural Experiment Station, as the Center was called for 83 years, was established at The Ohio State University, Columbus, in 1882. Ten years later, the Station was moved to its present location in Wayne County. In 1965, the Ohio General Assembly passed legislation changing the name to Ohio Agricultural Research and Development Center—a name which more accurately reflects the nature and scope of the Center's research program today.

Research at OARDC deals with the improvement of all agricultural production and marketing practices. It is concerned with the development of an agricultural product from germination of a seed or development of an embryo through to the consumer's dinner table. It is directed at improved human nutrition, family and child development, home management, and all other aspects of family life. It is geared to enhancing and preserving the quality of our environment.

Individuals and groups are welcome to visit the OARDC, to enjoy the attractive buildings, grounds, and arboretum, and to observe first hand research aimed at the goal of Better Living for All Ohioans!

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Ohio's major soil types and climatic conditions are represented at the Research Center's 13 locations. Thus, Center scientists can make field tests under conditions similar to those encountered by Ohio farmers.

Research is conducted by 15 departments on more than 6500 acres at Center headquarters in Wooster, nine branches, Green Springs Crops Research Unit, Pomerene Forest Laboratory, and The Ohio State University.

Center Headquarters, Wooster, Wayne County: 1953 acres

Eastern Ohio Resource Development Center, Caldwell, Noble County: 2053 acres

Green Springs Crops Research Unit, Green Springs, Sandusky County: 26 acres

Jackson Branch, Jackson, Jackson County: 344 acres

Mahoning County Farm, Canfield: 275 acres

Muck Crops Branch, Willard, Huron County: 15 acres

North Central Branch, Vickery, Erie County: 335 acres

Northwestern Branch, Hoytville, Wood County: 247 acres

Pomerene Forest Laboratory, Keene Township, Coshocton County: 227 acres

Southeastern Branch, Carpenter, Meigs County: 330 acres

Southern Branch, Ripley, Brown County: 275 acres

Western Branch, South Charleston, Clark County: 428 acres